

Evaluating biological control of yellow starthistle (*Centaurea solstitialis*) in California: A GIS based supply–demand demographic model

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Abstract

The biological control of yellow starthistle (*Centaurea solstitialis*) by four capitulum-feeding insects (weevils *Bangasternus orientalis* and *Eustenopus villosus*, and flies *Urophora sirunaseva* and *Chaetorellia succinea*), as affected by plant competition with annual grasses, is analyzed using a weather-driven, physiologically based, age-structured, simulation model. Seed density in the soil seed bank for yellow starthistle and the number of overwintering insects provide between-season links. Seed germination intensity and pattern is determined by the timing and quantity of autumn rains and temperatures, while season-length is mostly determined by soil–water balance. Output from the yellow starthistle systems model was integrated into a geographic information system to examine regional differences in abundance for all species across several ecological zones of California. A marginal analysis of the simulation results was performed to examine the efficacy of each capitulum-feeding insect, their within-capitulum competitive interactions, and the effect of competition from annual grasses on yellow starthistle populations. The model suggests that lack of complete control of yellow starthistle may be due to plant compensation via increased per-plant seed production at lower plant densities and the incomplete destruction of seed in attacked capitula. The model suggests herbivory that reduces the plant's ability to compensate and/or kills whole plants before seed maturity would most likely lead to control of yellow starthistle.

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Keywords: Yellow starthistle; Biological control; Weeds; Physiologically based modeling; GIS; Supply–demand model

1. Introduction

Yellow starthistle, *Centaurea solstitialis* L. (Asteraceae), is an invasive exotic weed throughout much of western North America. It is native to the Mediterranean region of southern Europe and was likely introduced as a contaminant in alfalfa seed into several temperate countries around the world, including Chile, Australia, and western North America (DiTomaso and

Gerlach, 2000). It was first recorded near the San Francisco bay in 1859 and now infests over 3 million hectares statewide in California alone (Maddox and Mayfield, 1985).

Yellow starthistle is a winter annual that invades rangelands, orchards, vineyards, pastures, parks, and natural areas. It is favored by soil disturbance, but is clearly capable of invading areas that have not been disturbed by humans or livestock for years including a number of relatively pristine nature preserves (J. Randall, The Nature Conservancy, Davis, CA, unpublished report; J. Sigg, California Native Plant Society, Sacra-

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mento, CA, personal communication). Dense infestations significantly deplete soil moisture in grasslands (Enloe et al., 2004) that result in mortality of more desirable grassland species, thereby reducing productivity of rangelands. Cattle avoid the spiny capitula, and the plant is toxic to horses (Corby, 1978). Infestations increase the frequency and intensity of fire. Considerable research on the use of herbicides, grazing management, fire, and biological control has occurred (DiTomaso et al., 2000).

Yellow starthistle has been the target of an ongoing biological control effort in the western USA. The first phase of this effort resulted in the release of six exotic insects that attack the capitula and their larvae feed on developing seeds. The first insect released was the gall fly, *Urophora jaculata* (Rondani) (Diptera: Tephritidae), in 1969, but it failed to establish (Turner et al., 1994). Five other insects were released from 1984 through 1992 and all have established. In California, three species are now widespread: *Bangasternus orientalis* (Capiomont) (Coleoptera: Curculionidae), *Eustenopus villosus* (Boheman) (Coleoptera: Curculionidae), and *Urophora sirunaseva* (Hering) (Diptera: Tephritidae). The two other insects, *Chaetorellia australis* (Hering) (Diptera: Tephritidae) and *Larinus curtus* Hochhut (Coleoptera: Curculionidae), occur in low numbers at a limited number of locations. A seventh insect, *Chaetorellia succinea* (Costa) (Diptera: Tephritidae), was accidentally introduced into southern Oregon in 1991 and is also widely established (Balciunas and Villegas, 1999). The combined impact of five of the insects (except *C. australis*) has been evaluated at three long-term study sites in central California (Pitcairn et al., 2002). The seed-feeding weevil, *E. villosus*, and the seed-head fly, *C. succinea*, are the most abundant and appear to cause the largest reduction in seed production. The other three insects occur in low numbers and appear to have little impact on seed production. Since 1995, seed production at the three study sites has continued to decline due to the steady annual increase in attack by *E. villosus* and *C. succinea* and, recently, a decline in the density of mature plants is beginning to be observed (Pitcairn et al., 2002).

Here we report on the development of a physiologically based, supply-demand, age-structured, simulation model to examine the interaction of yellow starthistle and the guild of capitulum-feeding insects in California. Specifically, the model is used to examine the factors that may lead to the success of yellow starthistle, to examine whether, given time, the introduced natural enemies can reduce plant abundance, and to examine whether seed destruction alone could eventually control yellow starthistle. The model is used to examine the efficacy of the introduced capitulum-feeding insects and to identify complementary or antagonistic interactions among them and yellow starthistle as modified by plant competition from annual grasses. The potential impacts

of the several natural enemies are first examined at Davis, California, then in other ecological zones of California. The latter is accomplished by integrating the yellow starthistle system model into a geographic information system (GIS).

1.1. Biology of yellow starthistle

Yellow starthistle is a winter annual that germinates with the onset of fall–winter rains in the northern hemisphere (Benfield et al., 2001). Yellow starthistle seedling populations often exceed 2000 per m² but self-thin to 200–800 per m². It occurs as a rosette during fall and winter and bolts in early spring when temperatures warm (Maddox, 1981; Roche and Thill, 2001). Flowering begins in early summer and, depending on soil moisture and temperature, may continue into the fall. Yellow starthistle is an obligate out-croser that requires pollination by bees to produce viable seed (Maddox et al., 1996; Sun and Ritland, 1998). The relationship between seed production and plant density under current levels of herbivory is shown in Fig. 1. Individual plants may produce from 1 to 100 capitula resulting in 650–700 capitula per m² during the season (Fig. 1A), but densities as high as 3000 capitula per m² have been reported (DiTomaso et al., 2003). On average, 625–650 degree-days (dd) are required for seed to mature (Fig. 1D).

Most seeds disperse within a meter of the parent plant (DiTomaso and Gerlach, 2000), but grazing animals and machinery can carry seed to much greater distances. Two kinds of seeds are produced: most are a light brown with short pappus and a lesser number of dark, non-pappus seed in a ratio of 5:1 (Roche and Thill, 2001). Most seeds are found on the soil surface or in the top 2 cm of soil (Joley et al., 1992). Seed survival has been estimated directly by burying mesh bags with seed at various soils depths and indirectly by monitoring the soil seed bank (Benfield et al., 2001; Callihan et al., 1993; Joley et al., 1992, 2003). The decline in the seed bank is due to germination, seed mortality, and predation. The loss rate is approximately 70–80% per year and results in a decline of 99% after 4 years (Benfield et al., 2001; Joley et al., 1992, 2003).

Four insects are widely established on yellow starthistle throughout California. Of these, *E. villosus* and *C. succinea* have the highest attack rates resulting in 30–90% of capitula attacked throughout the flowering season. The other two insects combined usually account for <10% of the attacks (Pitcairn et al., 2002). Depending on the species, 40–100% of seed in attacked capitula are destroyed (Pitcairn and DiTomaso, 2000). Prior to introduction of the capitulum-feeding insects, yellow starthistle produced approximately 30–40 seeds per head and resulted in yields of 50 million seeds per hectare (M.J. Pitcairn, unpublished data). Estimates of 120–500 million seeds per hectare have been recorded

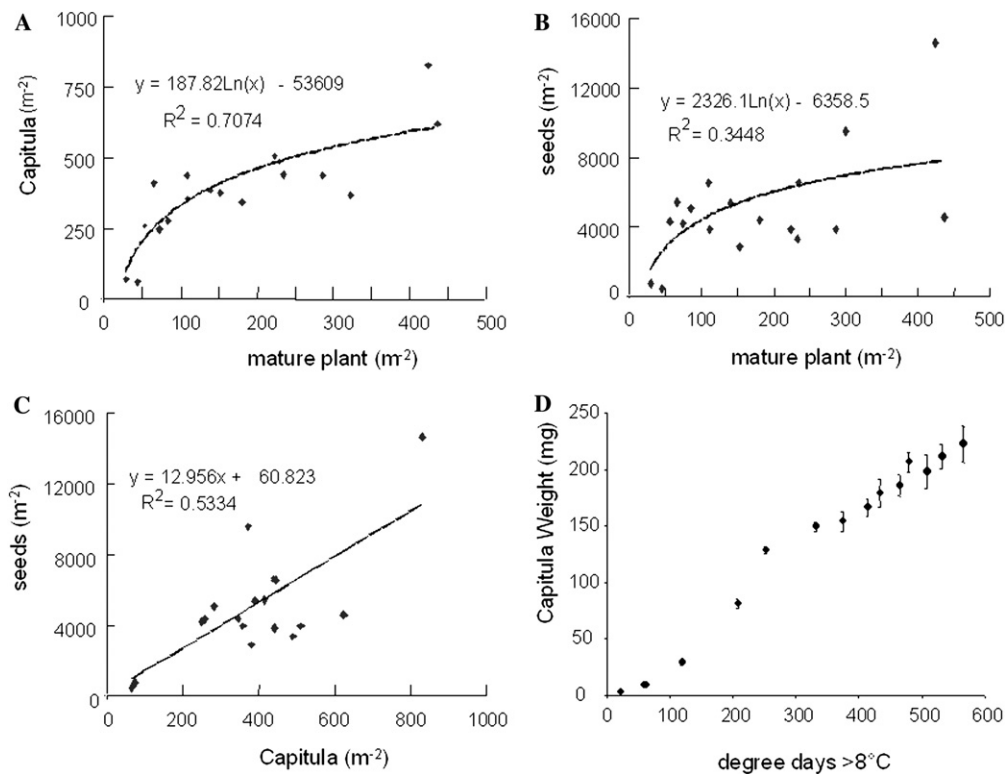


Fig. 1. Relationship between seed production and mature plant density: (A) capitula density vs. plant density, (B) seed density vs. plant density, (C) seed density vs. capitula density (from Pitcairn et al., 2002, for years 1995–2001, Placer, Solano, and Yolo Counties, California), and (D) capitulum dry mass as a function of degree-days (M.J. Pitcairn, unpublished data, Yolo County, California).

in heavily infested areas (DiTomaso and Gerlach, 2000; Maddox, 1981). Following introduction of the capitulum-feeding insects, annual seed production has decreased at three long-term study sites (Pitcairn et al., 2002).

1.2. Biology of capitulum-feeding insects

The weevils, *B. orientalis* and *E. villosus*, are univoltine and all adults produced during the season enter diapause. The tephritid flies, *C. succinea* and *U. sirunaseva*, have two to three generations per year with some individuals entering diapause in response to photoperiod below 13.5 h day length (N. Carruthers, unpublished data). In the model, we assume that the proportion entering diapause increases linearly with decreasing photoperiod in the interval 13.5–12.5 h day length. Those not entering diapause complete development and produce another generation when conditions are favorable. Further, we assume that approximately 5% of diapausing individuals survive the winter and emerge the following spring. In the model, the adults of all the insects emerge from winter diapause during spring in a sigmoid pattern displaced from each other to reflect observed patterns of field emergence (M.J. Pitcairn and N. Carruthers, unpublished data). The sex ratio for all four insects is assumed to be 1:1.

The preferences of the four insects differ by age and size of the capitulum (Fig. 2), and their developing larvae cause different amounts of per-capita damage to developing seed (*E. villosus* >> *B. orientalis* > *C. succinea* > *U. sirunaseva*). One may view these herbivores as parasites with possible super- and multiple-parasitism occurring within capitula. In cases of multiple attacks, we assume that *E. villosus* larvae are dominant to all other species, killing them in the process of its development. Successful development of multiple species (i.e., *B. orientalis*, *C. succinea*, and *U. sirunaseva*) may occur in the same capitulum although *C. succinea* is suggested to be partially dominant to *U. sirunaseva* (Fig. 2C).

The weevil, *B. orientalis*, lays its eggs on the surface of capitula where they are attacked by generalist predators at a rate of 30% per day (M.J. Pitcairn, unpublished data). The other three species lay their eggs within the seed head where they largely escape predation. A low intrinsic mortality rate is assumed for all herbivore immature stages (see Table 1).

1.3. Overview of the supply–demand model

Models of plant and pest systems have a long history in studies of agricultural production with important early roots in de Wit and Goudriaan (1978). Their goal

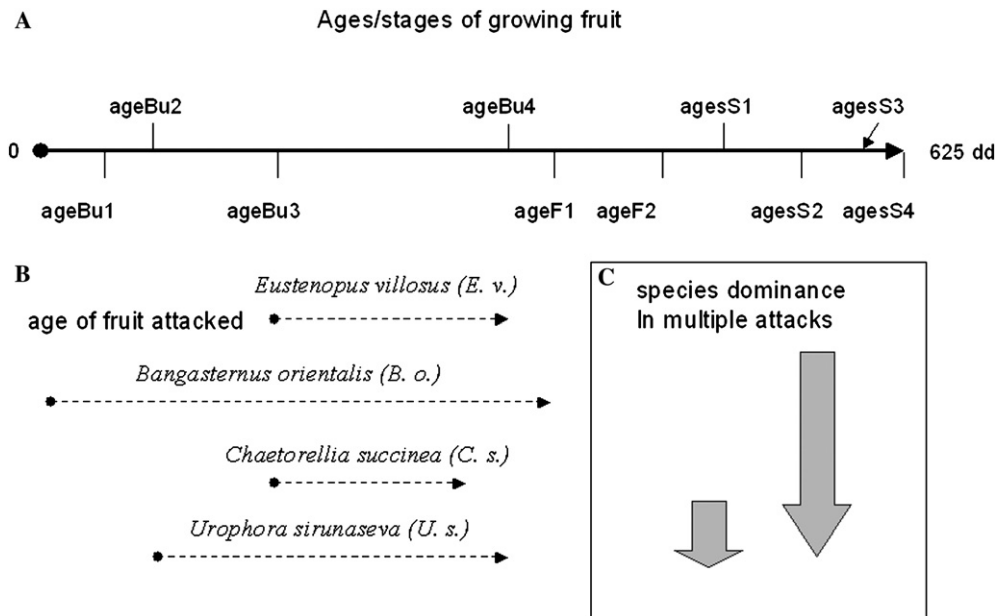


Fig. 2. Age of capitula (A) attacked by yellow starthistle natural enemies (B) and their dominance hierarchy in cases of multiple infestations of capitula (C).

was to capture the multitrophic perspective of plant–herbivore–natural enemy interactions to better manage resources and improve crop yield. A unified model for resource acquisition, allocation, and population dynamics across all trophic levels was developed for cotton (Gutierrez et al., 1991), alfalfa (Gutierrez and Baumgärtner, 1984), coffee (Gutierrez et al., 1998), cassava (Gutierrez et al., 1999), and others. The advantage of this approach is that the same model applies to all organisms despite their very different life histories and the models can be tested against field data. The basic premise is that all organisms face the same problems of resource (energy) acquisition and allocation. The model assumes an energy allocation priority: first to respiration (maintenance costs in economics), then to reproduction (profit) and, if assimilate (revenues) remains, to growth (infrastructure costs). These analogies allow us to use the same model to describe the dynamics of all interacting species within and among all trophic levels.

Each organism is assumed to try to satisfy a physiologically based demand for resources via the process of imperfect search causing the amount of captured resources (supply) obtained to be always less than the demand. Growth, reproduction, and survival rates are reduced from the maximum by the supply/demand ratio. Hence, biotic and abiotic factors affect either the supply (production) side or the demand (sinks, e.g., fruits) side of the supply/demand ratio. In some cases, both sides may be affected.

In construction, the systems model is modular with submodels for whole plants, plant subunits, and herbivores making up the constituent parts. Populations of

plants are composed of individuals of different ages (age-structure) and mass (mass structure) that vary over time. Each plant is composed of populations of subunits (i.e., of fruits, leaves, stem, and roots) that also have mass and age attributes and vary in attractiveness to herbivores.

Important supply-side herbivores include defoliators, sapsuckers, spidermites, nematodes, diseases, and other. These herbivores tend to reduce plant vigor, induce developmental delays, and reduce yields. Demand-side herbivores attack fruit (e.g., sinks) reducing their demand and reduce seed yield directly. Most plant species have a reproductive surplus that allows for varying degrees of compensation for such damage. Of crucial importance in compensation is the time and energy lost in the death of fruit. Little time and energy may be lost when buds and small fruit are killed and may be easily replaced. Attack on older fruit may involve considerable loss in time and energy often precluding compensation. Further information on this modeling approach is available in Gutierrez (1996).

2. Materials and methods

2.1. Development of the yellow starthistle systems model

To examine the interaction between yellow starthistle and its introduced capitulum-feeding insects, we modified the basic model developed for agricultural systems by using information specific to yellow starthistle and its herbivores for growth, reproduction, search, and survival. Some of this information was available in the

Table 1
Summary of parameters for the capitulum-feeding insects used in the yellow starthistle systems model

Species	<i>Bangastermus orientalis</i> (BO) (univoltine)	<i>Eustenopus villosus</i> (EV) (univoltine)	<i>Chaetorellia succinea</i> (CS) (multivoltine)	<i>Urophora sirunaseva</i> (US) (multivoltine)
Lower thermal threshold	9 °C	9 °C	9 °C	9 °C
Duration of egg stage (dd > 9 °C)	0–43	0–43	0–61	0–61
Duration of larval stage (dd > 9 °C)	44–148	44–148	61–209	61–209
Duration of pupal stage (dd > 9 °C)	149–223	149–223	209–315	209–315
Duration of preoviposition period (dd > 9 °C)	224–285	224–285	315–402	315–402
Duration of adult stage (dd > 9 °C)	286–1111 (85 days)	286–480 (20 days)	402–840 (27.8 days)	402–840 (27.8 days)
Area of search	0.75	0.75	0.75	0.75
Host feeding	0	2 per egg	0	0
Eggs per female—rate	0.41 per dd	0.89 per dd	0.34 per dd	0.34 per dd
Eggs per female—total lifetime	340	174	136–167	136–167
Larval behavior	Gregarious	Solitary	Gregarious	Solitary galls but multiple galls/head
Sex ratio	1:1	1:1	1:1	1:1
Mortality rate ^a , egg and larval stages	$x: = -0.5 * budsavl/R + 1.5$ $\mu_{larv} = 0.001332x$	$x: = -0.5 * budsavl/R + 1.5$ $\mu_{larv} = 0.001332x$	$x: = -0.5 * budsavl/R + 1.5$ $\mu_{larv} = 0.001332x$	$x: = -0.5 * budsavl/R + 1.5$ $\mu_{larv} = 0.001332x$
Mortality rate ^a , adult stage	$\mu_{larv} = 0.00972x$	$\mu_{larv} = 0.00972x$	$\mu_{larv} = 0.00972x$	$\mu_{larv} = 0.00972x$
Egg predation	30% per day (eggs laid externally)	0%	0%	0%
Immigration ^b —window	Plantdd < BStartdd + Bdurim	Plantdd < EVstartdd + EVdurim	Plantdd > CSstartdd + CSdurim	Plantdd > USstartdd + USdurim
Immigration ^b —rate per dd	$BO_{imm} = 0.5 * BO_{imrt} * Plantdda / Bdurim$	$EV_{imm} = 0.5 * EV_{imrt} * Plantdda / EVdurim$	$CS_{imm} = 0.5 * CS_{imrt} * Plantdda / CSdurim$	$US_{imm} = 0.5 * US_{imrt} * Plantdda / USdurim$
Emigration—rate per dd	$em = BOr[i] * (1.0 - \text{sqr}(BOSd))$	$em = EVr[i] * (1.0 - \text{sqr}(EVsd))$	$em = CSr[i] * (1.0 - \text{sqr}(CSSd))$	$em = USr[i] * (1.0 - \text{sqr}(USSd))$
Diapause—stage and induction factor	New adult stage	New adult stage	Pre-pupa—day length	Pre-pupa—day length
Fruit age preference	105–525 dd	315–425 dd	210–425 dd	105–315 dd
% seed destroyed per capitulum	50% Destroyed	>90%	70–100%	10% per gall

^a The number of small buds is budsavl; R is the total number of fruit; μ_{larv} is a measure of whether the plant is fruiting.

^b Immigration begins for each species during specific plant phenology periods and continues for a specified period ($Plantdd < (BnsStartdd + Bnsdurim)$).

literature and some was obtained in recent field studies specifically for this modeling effort.

The yellow starthistle systems model consists of 11 linked *functional populations*: a plant submodel with six, linked dynamics models: plant population (1), models for the mass of leaves (2), stem (3), and root (4) tissues, and for capitulum mass and numbers (5, 6), age-structured dynamics models for the four seed head insects, *B. orientalis* (7), *E. villosus* (8), *C. succinea* (9), and *U. sirunaseva* (10), and a model describing the impact of interspecific competition from annual grasses (11). The insect populations (7–10) are dynamically linked to the yellow starthistle capitulum models (5 and 6). The parameters for the insect and grass models are summarized in Table 1.

2.2. Mathematical details and assumptions

Here we describe the mathematics and assumptions of the critical components of the simulation model. Further details are available in Gutierrez (1996).

2.2.1. Population aging with distributed delay

Growth and development of all components were simulated using the Manetsch (1976)–Vansickle (1977) distributed maturation time model described here using the notation of DiCola et al. (1999, pp. 523–524). This model is characterized by the assumption

$$v_i(t) = v(t) = \frac{k}{\text{del}(t)} \Delta x, \quad i = 0, 1, \dots, k, \quad (1.1)$$

where k is the number of age intervals and $\text{del}(t)$ is the expected value of emergence time and Δx is an increment in age. From (1.1) we obtain

$$\frac{dN_i}{dt} = \frac{k}{\text{del}(t)} [N_{i-1}(t) - N_i(t)] - \mu_i(t)N_i(t), \quad (1.2)$$

where N_i is the density in the i th cohort and $\mu_i(t)$ is the proportional net loss rate. In terms of flux $r_i(t) = N_i(t) - v_i(t)$, yields

$$\frac{d}{dt} \left[\frac{\text{del}(t)}{k} r_i(t) \right] = r_{i-1}(t) - r_i(t) - \frac{\text{del}(t)}{k} \mu_i(t) r_i(t). \quad (1.3)$$

The model is implemented in discrete form (see Gutierrez, 1996).

2.2.2. Physiological time and age

The growth rates of yellow starthistle and the capitulum-feeding insects are directly related to the ambient temperature and hence, time and age in the model are in physiological time units (degree-days, dd). We assume the lower developmental threshold for yellow starthistle is 8 °C. We estimate the average rate of capitulum bud initiation at approximately 0.01 per dd > 8 °C and grow

to an average of 0.24 g dry mass over 575 dd (Fig. 1D) (M.J. Pitcairn, unpublished data). Laboratory studies suggest that the lower developmental threshold for *C. succinea* is 9 °C (N. Carruthers, unpublished data). The thresholds for the remaining herbivores are unknown and are assumed to be 9 °C. Because low temperatures are not limiting for development, this assumption does not affect the results of the model.

2.2.3. Resource acquisition

The biology of resource acquisition in all species involves search under conditions of time varying resource ($R(t)$) and temperature dependent per capita demand rates ($D_n(T(t))$) of a population of consumers ($C_n(t)$). Resource acquisition ($S(t)$) is modeled using the ratio-dependent modified-random search Gutierrez-Baumgärtner model (Eq. (2); Gutierrez, 1992).

$$S(t) = D_n C_n h_n(u) \\ = D_n(T(t)) C_n(t) \left[1 - \exp \left(\frac{-\alpha_n R(t)}{D_n(T(t)) C_n(t)} \right) \right]. \quad (2)$$

The function $h_n(u)$ is the proportion of the demand $D_n(T(t)) C_n(t)$ obtained by the n th population and (α_n) is the search parameter. Intraspecific competition enters the model via the exponent as the ratio of resource to population demand. Age (j) specific host preference coefficients ($0 \leq \xi_{n,j} \leq 1$) are incorporated in Eq. (3) by modifying $R_n(t)$ as follows:

$$R_n(t) = \sum_{j=1}^j \xi_{n,j} R_{n,j}(t). \quad (3)$$

For the yellow starthistle system, growth rates and dry-matter partitioning were based on field studies. Fig. 3A shows observed dry matter growth in different plant sub-units under nonlimiting conditions, Fig. 3B shows the relationship of capitula dry matter to vegetative dry matter, and Fig. 3C shows the partitioning ratios. Estimates for maximum plant growth rates in the model were derived from these data.

The capitulum-feeding insects oviposit in or on capitula behaving much like parasites as they destroy only part of the seed. The maximum per capita demand rate for oviposition sites is age (a) dependent and is estimated using Eq. (4) where b and c are fitted constants.

$$D_n(a, t(T)) = \frac{ba}{c^a}. \quad (4)$$

The population demand is summed across all age classes $i = 1, k$ (Eq. (5)) and corrected for sex ratio (ϕ_n).

$$D(T(t)) = \phi_n \cdot \sum_{i=1}^{k_n} D_{n,i}(a = i, t(T)) C_{n,i}(t). \quad (5)$$

Whatever the species, time-varying variables $R_n(t)$ and $D(T(t))$ enter the functional response model Eq. (2) to estimate the realized resource acquisition rate ($S(t)$).

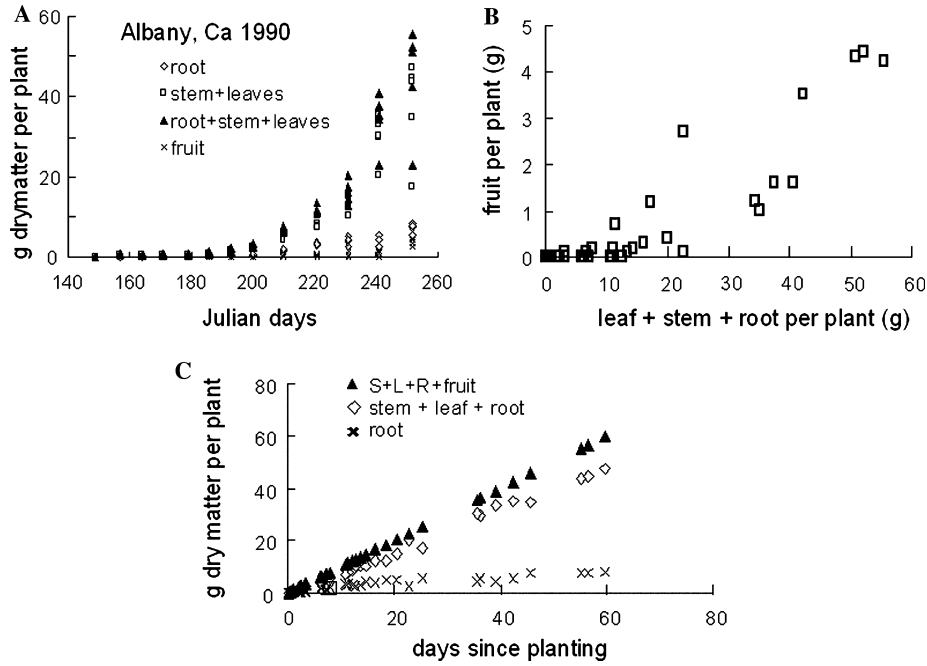


Fig. 3. Dry matter production and allocation for yellow starthistle growing at Albany, CA, during 1990: (A) growth of plant subunits, (B) the relationship between capitula mass and vegetative mass, and (C) dry matter allocation.

When multiple herbivore species are interacting, the number of attacked and healthy capitula, as modified for preference, are included as the resource and, with their total demand, are included in Eq. (2) to estimate the maximum number of capitula attacked by all species (S). Next, the independent attack rate of each insect species ($S_1^*, S_2^*, S_3^*, S_4^*$) is computed again including capitula previously attacked by other herbivores. The actual number of capitula attacked by each species (S_n) is the proportion of the summed independent rates [e.g., ($S_1^*/(S_1^* + S_2^* + S_3^* + S_4^*)$)] multiplied by S corrected for preference and dominance in cases of multiple “parasitism” (see Mills and Gutierrez, 1996).

2.2.4. Supply–demand effects

Resource acquisition success is estimated by the supply/demand ratio ($\phi_{S/D,n}(t)$) obtained by dividing both sides of Eq. (2) by the appropriate population demand ($D_n C_n$).

$$0 \leq \phi_{S/D,n}(t) = h_n(R_n(t), C_n(t)) = \frac{\text{supply}}{\text{demand}} < 1. \quad (6)$$

Some species may have multiple resource demands that together affect the success of the species in the area. For example, light, water, and nutrients may be independently limiting for yellow starthistle, and their effect may be exacerbated by competition with annual grasses.

Light acquisition by yellow starthistle was estimated by assuming that the total light falling per unit of ground (cal per m² per day) at time t is $R = \psi(t)$, hence the light available to yellow starthistle ($\psi_{YST}(t)$) is the fraction of the total leaf area index (LAI) it represents.

$$\psi_{YST}(t) = \psi(t) \cdot \text{LAI}_{YST}(t) / (\text{LAI}_{YST}(t) + \text{LAI}_{grass}(t)) \quad (7)$$

$\psi_{YST}(t)$ is multiplied by a constant to convert it to gram dry matter. The search parameter α_n is a concave function of LAI ($\alpha_n(\text{LAI}_{YST})$). The variables, $\psi_{YST}(t)$, α_n , and the demand rate, are used in Eq. (2) to compute the photosynthetic rate as affected by a reciprocal competition with grass. The success of yellow starthistle in meeting its demand is measured by its photosynthate supply/demand ratio (e.g., ($0 \leq \phi_{S/D}(t) = S(t)/D(t) < 1$)) (Eq. (6)). The photosynthetic rate may, however, be modified by shortfalls in other factors such as water (w) and nutrient (η) stress. The combined effect of all essential resources is captured as the product of the independent supply–demand ratios (Eq. (8)).

$$\phi^*(t) = \phi_{(S/D)} \phi_{(w)} \phi_{(\eta)} \dots \quad (8)$$

Eq. (8) is functionally Liebig’s Law of the Minimum because when any component of $\phi^*(t)$ falls below a limiting value, it becomes the limiting factor. Hence, multiplying the population demand $D_n(t)C_n(t)$ by $\phi^*(t)$ estimates the photosynthate produced under specific environmental conditions and allocated in priority order to respiration, conversion costs, reproduction, and vegetative growth (see Gutierrez, 1992, 1996).

Similarly, the supply–demand ratio approach is used to model the insect species attacking yellow starthistle. For example, shortfalls in the number of capitula affect oviposition rates and increase adult insect emigration. Shortfalls are particularly significant for *C. succinea* that

emerges in early spring before large numbers of capitula are available in the field (Pitcairn, 2002). The adult flies are relatively long-lived but emigration of adults is a source of mortality to the local population.

2.2.5. Phenology

In fall, germinating seed in the soil seed bank initiate yellow starthistle populations and, in spring, adult capitulum-feeding insects emerge from diapause to initiate their populations. We assume that each year (y) approximately 72% of the seed ($v(y, t_0)$) in the soil die from various causes and 8% may germinate ($v^*(y, t_0)$). The remaining 20% remain in the soil to die or germinate in subsequent years. The daily germination rate ($\phi(t, r(t))$) depends on the intensity of daily (t) rainfall ($\text{mm}(t)$).

$$\phi(y, t, \text{mm}(t)) = v^*(y, t)[1 - \exp(-0.04 \text{mm}(t))]. \quad (9.1)$$

The available seed bank density declines during the season as

$$v^*(y, t + 1) = v^*(y, t) - \phi(y, t, \text{mm}(t)). \quad (9.2)$$

The total seed available next year consists of the unavailable fraction ($0.2v(y, t_0)$) and the seed that had not germinated by the end of the season ($t = t^*$) (i.e., $v^*(y, t^*)$) plus the within-season recruitment ($\Delta v(y)$) (Eq. (10))

$$v(y + 1) = 0.2v(y, t_0) + v^*(y, t^*) + \Delta v(y). \quad (10)$$

2.2.6. Mortality of seedlings from fungal attacks

Seedling mortality is high (50–70%) due, in part, to soilborne pathogens that are active during the fall–spring rainy season. Mortality due to fungi ($\mu_{\text{pathogen}}(t)$) occurs in the seedling and rosette stages at rates that are a function of daily rainfall intensity (Eq. (11)).

$$\mu_{\text{pathogen}}(t) = 1 - \exp(-0.025 \text{mm}(t)). \quad (11)$$

Note that the mortality component is similar to the germination rate (Eq. (9.1)), but the number dying is a proportion of the seed that germinated. Fungal mortality declines with plant age and as rains diminish in spring (Pitcairn et al., 2000).

2.3. Simulations and analyses

Simulation analysis was first conducted for Davis, Yolo County, California to explore the interaction of the system components over time. Next, the models were integrated into a GIS based on ESRI ARC/Info 8, and used in an analysis across other ecological zones in California. Weather (e.g., daily maximum–minimum temperatures, solar radiation, precipitation, wind, and relative humidity) was used to drive the dynamics of the model (University of California Integrated Pest Management Project (UCIPM)).

Model simulations for Davis, California, for the 1982–1983 and 1989–1990 seasons were used to illustrate plant phenology and survival, while simulations for 20 continuous years (15 September 1982–15 September 2003) were used to analyze the factors affecting yellow starthistle abundance. Simulations were run sequentially for yellow starthistle alone and with all combinations of the four herbivores and annual grasses. Initial conditions were unknown; hence, the first-year simulation was started with an initial seed bank of 4500 seeds per m^2 , an initial density of five diapause individuals per m^2 of each insect species and nonlimiting soil moisture. In subsequent years, the germination of yellow starthistle at the beginning of the season depended on the number of viable seed in the soil, while soil moisture and the number of overwintering insects were carried over from the previous season.

The regional GIS analysis used 72 locations having complete weather data for the period 1 January 1995–25 September 2003. The initial values for Davis, California, were used at all sites because field estimates were not available. Initial soil moisture at each location was estimated as the final value at each location from a dry run of the system. Daily outputs of the model were generated, but only end-of-season summary results were analyzed and mapped. GIS triangulation kriging methods were used to interpolate the data for mapping.

2.4. Marginal analysis

Multiple linear regression analysis of the simulation data was used to assess the impact of weather and the capitulum-feeding insects on measures of plant and insect abundances. All regressions used as independent variables the season length, cumulative rainfall during the season, and the presence–absence of grass and capitulum-feeding insects. Only independent variables and interaction terms with slopes significantly different from zero (t -values with $P < 0.05$) are reported. We recognize the statistical problems inherent in analyzing simulation data in this way, but the goal is only to assess general trends and relationships in the model output. The goal is not prediction, as measured by explained variance, nor is it to determine statistical differences among the independent variables. Rather, this method seeks only to estimate the average magnitude and direction of large effects on plant and insect abundance. The analysis measures the average marginal effect of a factor (x) on a dependent variable, given the average effect of all other factors retained in the regression. The effect on the dependent variable is estimated by the partial derivative with respect to the independent variable. This approach was used successfully in the analysis of the biological control of the cassava mealybug (Neuenschwander et al., 1989).

3. Results

3.1. Site-specific analysis—Davis, California

Simulated germination and subsequent developmental phenology and survival of yellow starthistle at Davis, California, during the 1982–1983 and 1989–1990 seasons (hereafter referred to as 1983, 1990) are shown in Figs. 4A and B, respectively. The decline in plant numbers later in the season includes the supply–demand effects of inter- and intraspecific competition for light

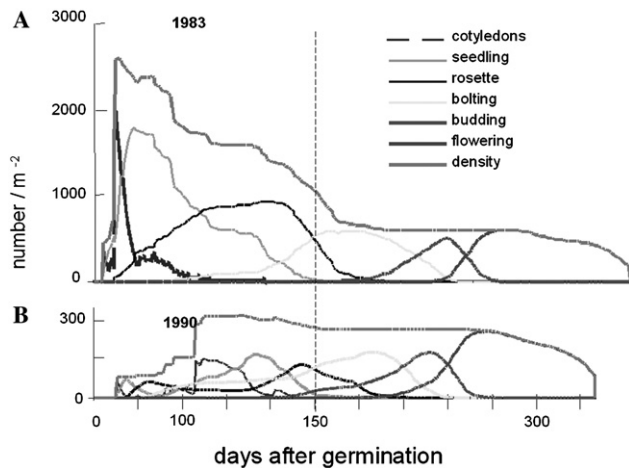


Fig. 4. Simulated yellow starthistle plant phenology during 1982–1983 and 1989–1990 seasons at Davis, California. The vertical dotted line indicates the start of budding.

and water. Germination during 1983 was more synchronized producing nine times more seedlings than in 1990. In 1990, roughly 270 mature plants from an initial 300-seedling per m^2 survived, while in 1983 roughly 450 of the 2600 seedlings survived. The 1983 season was wetter than 1990 resulting in more disease and a longer growing season.

The range of seedling densities across the 20 seasons at Davis, California, was roughly 6-fold (Fig. 5A). Low seedling densities during some years were due to lower seed bank densities and not to low rainfall and/or the depletion of available soil water during the growing period (Fig. 5B). Reduction in mature yellow starthistle plant densities from competition with annual grasses was roughly 20–25% (Fig. 6A vs. B) with the added effects from the seedling diseases and capitulum-feeding insects being an additional 20–25% (Fig. 6C). These results are qualitative making it difficult to separate the biotic effects from those of weather. For this reason, we used marginal analysis to examine the interactions further.

3.2. Marginal analysis—Davis, California

3.2.1. Seed bank density

Depletion of seed bank density is thought to be essential for the suppression of yellow starthistle populations. The contribution of the presence–absence (0,1) of the different herbivore is estimated in Eq. (12). The model estimated that seed bank numbers were decreased 27% by the combined action of the herbivores.

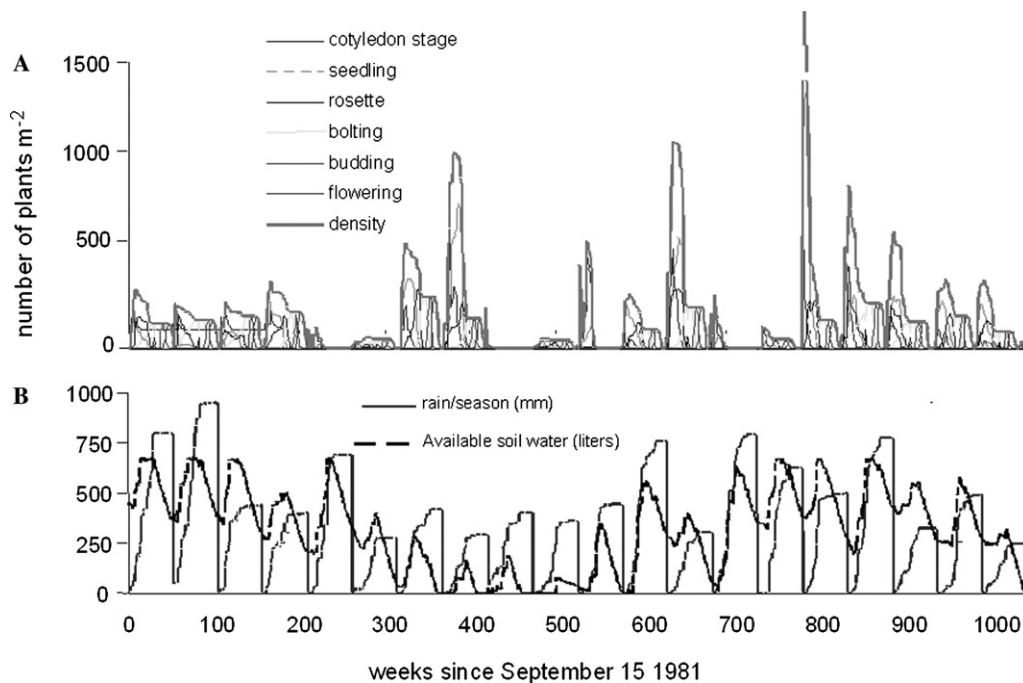


Fig. 5. Twenty years of yellow starthistle simulation results for Davis, California: (A) phenology and survival patterns of yellow starthistle per m^2 by growth stage and (B) total season rainfall and available soil water (liters per 2 m^3).

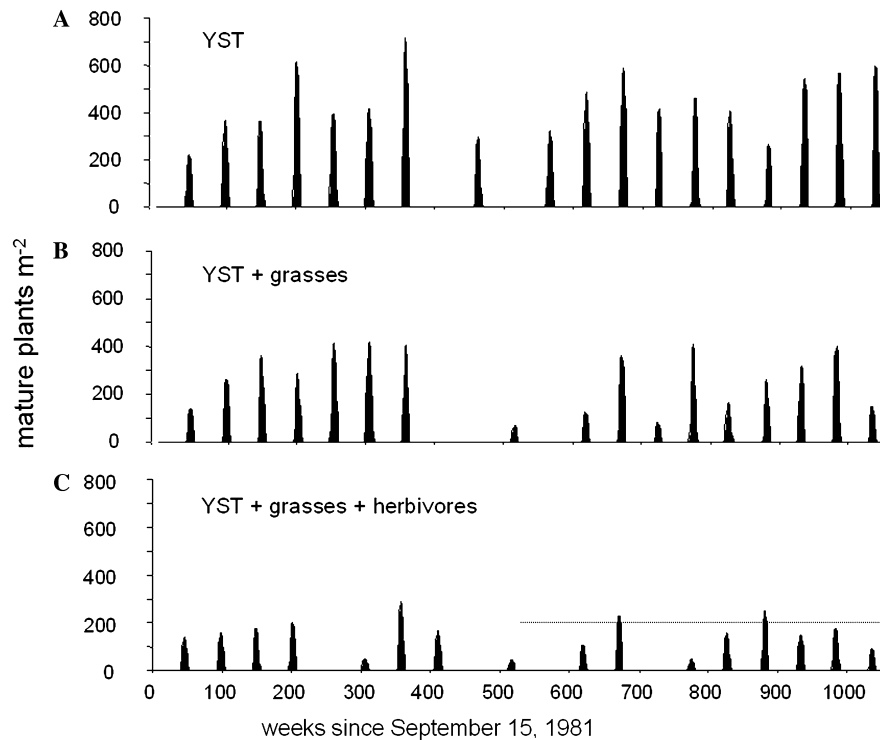


Fig. 6. Simulation of 20 years (1982–2002) of yellow starthistle populations at Davis, California, showing the pattern of surviving mature plants: (A) yellow starthistle alone, (B) yellow starthistle with competition from annual grasses, and (C) the added effects of all natural enemies. The horizontal line is the standard reference level for comparison across treatments (A–C) and across years within treatments.

$$\begin{aligned} \text{seed bank} = & 6763.3 - 3376.7Bo - 3110.9Ev - 2995.5Cs \\ & - 1297.0Us + 2393.9BoEv + 950.34BoCs \\ & + 987.3BoUs + 1033.5EvCs + 496.6EvUs \\ & + 492CsUs, \end{aligned} \quad (12)$$

$$R = 0.64, \quad F = 38.6, \quad df = 589,$$

where *Bo* is *B. orientalis*, *Ev* is *E. villosus*, *Cs* is *C. succinea*, and *Us* is *U. sirunaseva*. The regression model suggests that singly *B. orientalis*, *E. villosus*, and *C. succinea* could reduce seed bank densities 45–48% with their competitive interactions reducing total herbivore effectiveness roughly 20%. Specifically, this suggests that seed bank levels at Davis might be lower in the absence of *B. orientalis* and *U. sirunaseva*. In the field, *B. orientalis* and *U. sirunaseva* densities are very low and are thought to play minor roles in suppressing yellow starthistle's seed bank levels (Pitcairn et al., 2003). The model estimates that *U. sirunaseva* alone would likely reduce seed bank densities only 19%. Average seed bank levels after the action of all species would be 2345 per m² or a 65% reduction from the expected value without herbivores. Competition from annual grasses, rainfall, and season length were not significant factors in this analysis.

3.2.2. Mature plant density

The density of mature flowering plants per square meter is a measure of the current standing vegetative

crop, but its reduction is not necessarily a measure of control as fewer plants may mean larger plants with more seeds per plant. Using mature plant density as the dependent variable and regressing it against insect and grass presence (*G*) yields regression equation (13).

$$\begin{aligned} \text{mature plant density} = & 370.6 - 74.4Bo - 79.6Ev \\ & - 66.8Cs - 123.5G \\ & + 66.6BoEv + 22.5BoCs, \end{aligned} \quad (13)$$

$$R = 0.27, \quad F = 36.3, \quad df = 593.$$

In the absence of biotic constraints, the model estimates that mature plant densities would stabilize at 370 plants per m². The regression equation suggests that *E. villosus* and competition from grasses reduce yellow starthistle densities 21 and 33%, respectively, resulting in average flowering densities of about 166 per m². The added effects of *C. succinea* and *B. orientalis* would reduce plant densities further to 115 per m², a density that is still quite high. The interactions of *BoEv* and *BoCs* increase yellow starthistle densities, suggesting that *B. orientalis* contributes little to control.

3.2.3. Capitula density

The number of capitula per square meter increases with season length (dd) and cumulative season long rainfall (mm), but is reduced by *E. villosus* because the adults feed on young capitula buds.

$$\begin{aligned} \text{capitula} = & 218.94 + 0.033 \text{ dd} + 0.37 \text{ mm}_{\text{rain}} \\ & - 229.6Ev, \end{aligned} \quad (14)$$

$$R = 0.34, \quad F = 102, \quad df = 596.$$

If the average dd is 2368 degree days $>8^\circ\text{C}$ and the average total rainfall is 512 mm, then including *E. villosus* reduces potential capitula density 47% to 351.2 capitula per m^2 .

3.2.4. Seed production

The regression for seed production mirrors that for capitula density with the added effect of competition from grass.

$$\begin{aligned} \log_{10}\text{seed density} = & -1.85 + 0.002 \text{ dd} \\ & + 0.0012 \text{ mm}_{\text{rain}} - 0.382Ev \\ & - 0.207G, \end{aligned} \quad (15)$$

$$R = 0.72, \quad F = 346.3, \quad df = 531.$$

E. villosus decreases seed densities 58% and competition from grasses reduces it 38%, with the combined reduction rate being (0.74).

3.2.5. Interspecific competition among herbivores

The interactions of the four capitulum-feeding insects were examined using \log_{10} cumulative larval days during the season (i.e., abundance is represented as cumulative larval days) for each species as the dependent variable and their presence-absence and the interactions terms as the independent variables.

3.2.5.1. *Bangasternus orientalis*. Only the presence of *E. villosus* has a significant but large negative effect on *B. orientalis* abundance. Taking the antilog of the model results estimates that, without *E. villosus*, cumulative *B. orientalis* larvae would be 1096 per m^2 , but with *E. villosus* it drops to 3.5 per m^2 .

$$\begin{aligned} \log_{10}Bo = & 3.04 - 2.5Ev, \end{aligned} \quad (16)$$

$$R = 0.61, \quad F = 144.2, \quad df = 271.$$

3.2.5.2. *Eustenopus villosus*. The effects of competition from *B. orientalis*, *C. succinea*, and *U. sirunaseva* on $\log E. villosus$ were not significant, but the indirect effects of grass competition on YST growth and hence capitula production did reduce *E. villosus* abundance (794 per m^2) by 23%.

$$\begin{aligned} \log_{10}Ev = & 2.90 - 0.1154G, \end{aligned} \quad (17)$$

$$R = 0.3, \quad F = 9.6, \quad df = 318.$$

3.2.5.3. *Chaetorellia succinea*. Only *E. villosus* reduced *C. succinea* abundance on average by 62%.

$$\begin{aligned} \log_{10}Cs = & 3.93 - 0.416Ev, \end{aligned} \quad (18)$$

$$R = 0.46, \quad F = 12.48, \quad df = 258.$$

3.2.5.4. *Urophora sirunaseva*. Only *E. villosus* and *C. succinea* decreased *U. sirunaseva* larval abundance with *C. succinea* having the larger effect Eq. (19).

$$\begin{aligned} \log_{10}Us = & 4.03 - 1.46Ev - 1.91Cs + 0.63EvCs, \end{aligned} \quad (19)$$

$$R = 0.56, \quad F = 125.9, \quad df = 296.$$

The *EvCs* interaction is positive thereby increasing *U. sirunaseva* abundance, but only slightly. In the absence of competitors, *U. sirunaseva* abundance would be 10,715 per m^2 , but with competition, it is reduced to 19.5 per m^2 because both *E. villosus* and *C. succinea* are superior competitors in cases of multiple parasitism of capitula.

3.3. Regional GIS analysis

The objective of the GIS analysis is to examine the expected level of biological control of yellow starthistle after 8 years at 72 sites across several climatic regions of California. The GIS analysis is limited to those regions for which sufficient weather data were available, principally the primary agricultural regions of central and southern California.

3.3.1. Yellow starthistle

The expected mature flowering plant and capitula density are illustrated in Figs. 7A, and B, respectively, showing that the areas unfavorable for yellow starthistle growth are the very hot, dry areas (see also Maddox and Mayfield, 1985). Germination in dry areas is compromised by infrequent rain while water stress determines the length of the growing season for the few seeds that germinate. The cumulative effect of several dry seasons limits the expected density and distribution of the weed. Seed bank densities in the soil at the beginning of the eighth season range from 70 to 5865 seed per m^2 (Fig. 7C) among locations, while the total within-season seed production ranged from 11 to 29,400 per m^2 (Fig. 7D).

Plots of the expected densities for the four capitulum-feeding insects (Fig. 8) showed that *B. orientalis* and *U. sirunaseva* would likely occur in very low numbers region-wide and were not included further in the regional analysis of yellow starthistle. The regression model of \log_{10} seed bank density across all 72 sites on season length (dd), total rainfall (mm), *E. villosus* and *C. succinea* is Eq. (20).

$$\begin{aligned} \log_{10}\text{seed density} = & 3.30 + 0.00007 \text{ dd} \\ & + 0.0002 \text{ mm} - 0.18Ev \\ & - 0.36Cs + 0.16EvCs, \end{aligned} \quad (20)$$

$$R = 0.42, \quad F = 141.4, \quad df = 3234.$$

The regression equation suggests that, on average, yellow starthistle seed densities increased with season length and total rainfall but decreased with the presence of *E. villosus* and *C. succinea*. The combined action of

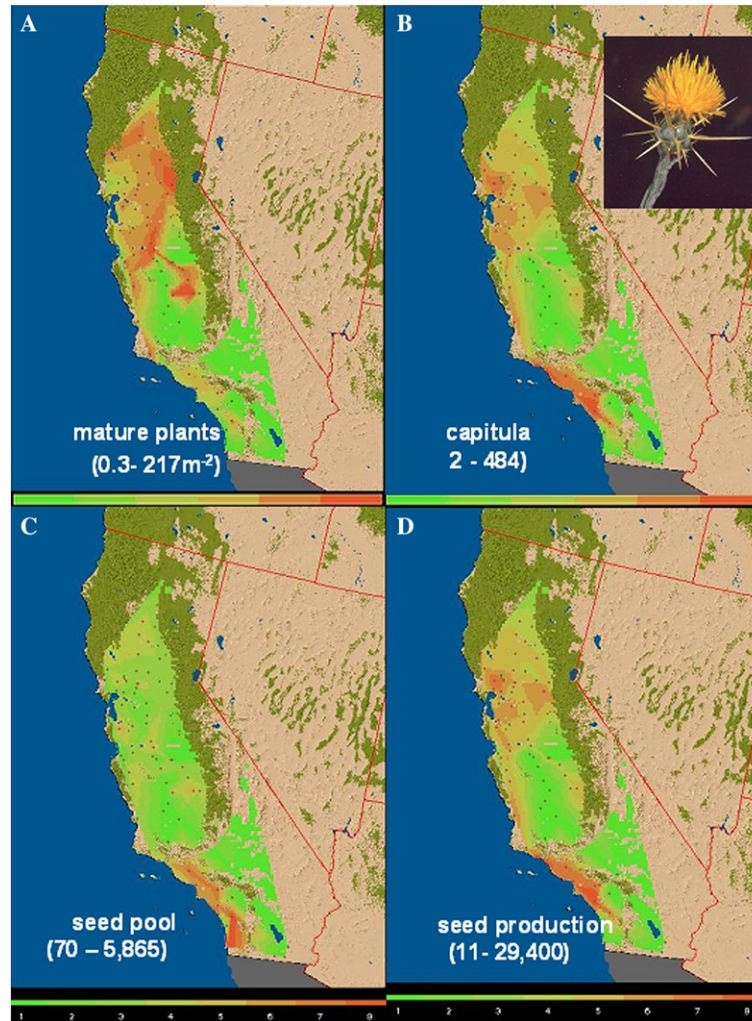


Fig. 7. GIS maps below 1000 m of: (A) maximum vegetative dry matter (g per m^2), (B) maximum capitula per m^2 , (C) seed pool per m^2 at the beginning of the growing period, and (D) seeds per m^2 on the final year of an 8-year simulation (September 1995–September 2003) using weather from 72 locations. The color red indicates higher densities, green lower densities. The + symbol in the maps are the locations of weather stations.

E. villosus and *C. succinea* reduced seed production on average 58% across the entire region with *C. succinea* having the greatest impact. The impact of *C. succinea* is reduced by its interactions with *E. villosus* because the weevil larva kills fly larvae when they co-occur in capitula. The *EvCs* interaction increased seed survival 12.8% offsetting much of *Ev*'s contribution.

Mature flowering plant densities declined with abiotic factors that increased season length (dd, mm) as well as *E. villosus*, *C. succinea*, and competition from annual grasses.

$$\begin{aligned} \text{mature plant density} = & 219.4 - 0.012 \text{ dd} - 0.01 \text{ mm} \\ & - 12.0Ev - 30.0Cs \\ & + 8.6EvCs - 7.9G, \end{aligned} \quad (21)$$

$$R = 0.22, \quad F = 27.6, \quad df = 3233.$$

Again, the *EvCs* interaction decreased biological control (i.e., increased plant density). Using average dd and mm,

average mature plant density was estimated to be 142 per m^2 across the entire region.

The number of capitula per m^2 increased with season length (dd), cumulative rainfall (mm), and *C. succinea* presence, but was greatly reduced by *E. villosus* presence with the contribution of the *EvCs* interaction playing a minor role.

$$\begin{aligned} \text{capitula density} = & 171.8 + 0.052 \text{ dd} + 0.16 \text{ mm} \\ & - 105.3Ev + 22.3Cs - 29.8EvCs, \end{aligned} \quad (22)$$

$$R = 0.53, \quad F = 248.6, \quad df = 3234.$$

Again, using average values for dd and mm, average capitula density across the entire region was estimated to be 271 per m^2 .

3.3.2. Cumulative overwintering insect stages

The number of overwintering insects in the final year of simulation was used as a metric of activity after the

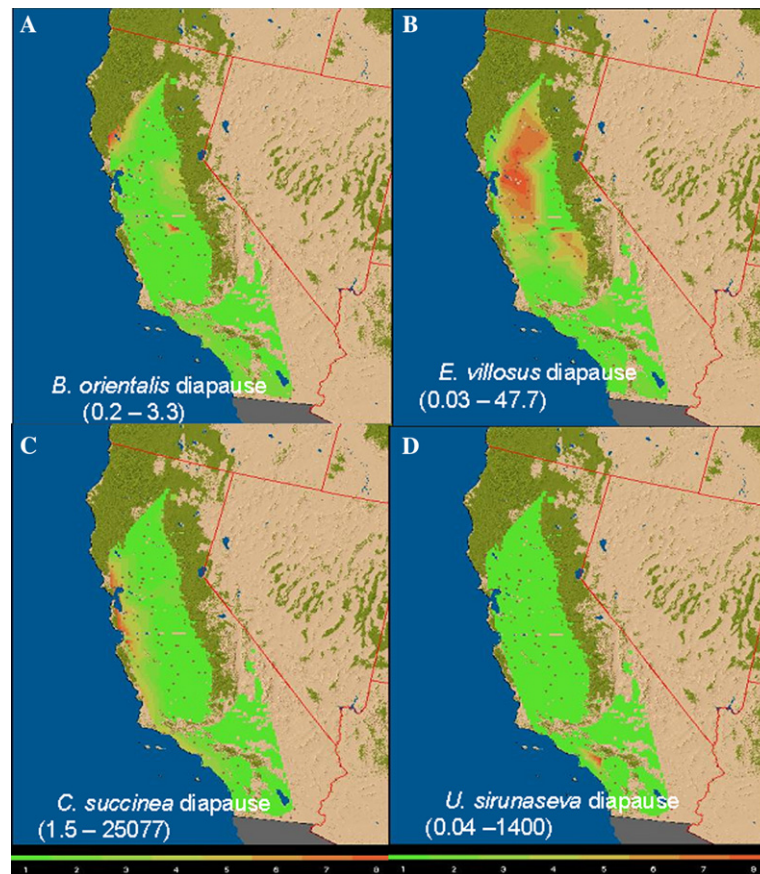


Fig. 8. GIS maps below 1000 m for total larvae per m²: (A) *Bangasternus orientalis*, (B) *Eustenopus villosus*, (C) *Chaetorellia succinea*, and (D) *Urophora sirunaseva* on the final year of an 8-year simulation (September 1995–September 2003) based on weather from 72 locations. The color red indicates higher densities, green lower densities. The + symbol in the maps are the locations of weather stations.

system “equilibrated” over eight seasons (Fig. 8). The weevil, *E. villosus*, was estimated to have the widest distribution but occurred largely across the wetter, more northern areas of California (Fig. 8B). The fly, *C. succinea*, had a more coastal distribution where high numbers are suggested to occur (Fig. 8C). The regional abundances of *B. orientalis* and *U. sirunaseva* were generally very low (Figs. 8A and D), but were high in a few very restricted areas of California.

4. Discussion

It is clear that yellow starthistle is a very successful invasive weed in California. Maddox and Mayfield (1985) estimated its infestation area at 3.2 million hectares, but since then it has increased to over 4 million hectares (DiTomaso and Gerlach, 2000). Biological control of yellow starthistle has been attempted using several insects that attack the capitula and reduce seed production. While most of these introduced species have established, it was not known if any or all species thrive in all ecological zones where the plant grows in California and, if so, the level of control they provide. The ability of herbi-

vores to control plant populations by destruction of seed alone has been questioned by several researchers because density-dependent mortality of seedlings and compensation by surviving plants can negate the loss of seed to herbivory (Crawley, 1983; Harper, 1977). Myers and Risley (2000) used a simulation model to examine the interaction of *Centaurea diffusa* Lam. and its various biological control agents introduced for its control in North America. Their results suggested that even at seed destruction rates over 95%, *C. diffusa* plant populations failed to decline, and possibly increased due to density-dependent compensation by the plant. Similarly, Hoffmann (1990) modeled the interactions of three biological control insects of the tree, *Sesbania punicea* (Cav.) Benth., in South Africa, and predicted that control by seed destruction alone was possible only at levels above 95%. Hoffmann’s analysis suggested that a stem-borer could control *S. punicea*, but the resulting populations would experience large fluctuations in density. The addition of the seed feeders dampened the oscillations suggesting that the most effective control would result from the combined impact of all of the herbivores.

In contrast, other models of plant–herbivore dynamics suggest that seed destruction can lead to declines of

plant densities. Shea and Kelly (1998) developed a matrix model to assess the impact of *Rhinocyllus conicus* (Froelich) on its target host, *Carduus nutans* L., in New Zealand. They estimated that seed losses greater than 69% of annual production would result in control. However, *R. conicus* destroys only 30–40% of seed in the field in New Zealand and it alone fails to control this weed. In North America, *C. nutans* populations were reduced after introduction of *R. conicus* (see Kok, 2001) possibly due to the higher levels of seed destruction observed there.

Rees and Paynter (1997) developed a simulation model for the invasive shrub, *Cytisus scoparius* (L.) Link, in Australia. Results from their model suggested that soil disturbance, rate of senescence, and local recolonization had the greatest impact on plant population dynamics. Seed feeders causing 75% reduction in seed production may have significant impact, especially in inherently highly disturbed habitats such as river corridors or areas subject to mechanical control.

In our yellow starthistle systems model, plant compensation occurs at low density as a consequence of reduced intraspecific competition for light and water. Simulation results suggest that high seed production allows yellow starthistle populations in California to reach carrying capacity rapidly and to remain dominant in the annual plant community. Once at carrying capacity, mature yellow starthistle populations are limited primarily by annual amounts of rainfall and season length in degree-days. The effects of nutrients were not included in our analysis because data on initial conditions were unavailable, but they have been shown to increase seed production (D. Spencer and S. Enloe, USDA-ARS Aquatic Weeds Laboratory, Davis, CA, personal communication). Competition from annual grasses appears to have limited impact on yellow starthistle dominance in an invaded plant community because they complete their life cycle by late spring and compete with yellow starthistle for only a portion of its life cycle. Once grasses have senesced, yellow starthistle is free to reproduce without further direct competition (Dukes, 2001). Still, the effect of grasses on yellow starthistle growth during the seedling and rosette stages is significant, increasing mortality and reducing seed production in survivors, but this alone is not enough to reduce significantly yellow starthistle mature plant density. Competition from grasses reduced yellow starthistle seedling survival 40–50% following and during dry years, but it also affected annual variations in yellow starthistle seedling density during most years. All of these results are consistent with field observations that show that once an area is invaded, yellow starthistle populations persist.

Analysis of the attack by the four capitulum-feeding insects suggests that two of the four likely cause most of the impacts observed in the field. The combined attack of all the insects resulted in a 58% reduction in

regional yellow starthistle densities but the attack by the weevil, *E. villosus*, and the fly, *C. succinea*, were the major contributing factors with competition from grasses being significant at some locations (e.g., Davis, CA) but not across the entire region. The simulation results at Davis, California, suggest that *E. villosus* has the largest direct impact on the coexistence of the other biological control agents via its dominance in cases of multiple parasitism of capitula and indirectly via the destruction of young buds during host feeding. However, multi-year simulations suggest that population levels of *E. villosus* will not be significantly higher than currently observed in the field. Although high populations of *C. succinea* occur in some areas and/or years when synchrony with yellow starthistle is enhanced by weather and where competition with *E. villosus* is low, *C. succinea* is generally poorly synchronized with its preferred host stage during its spring emergence.

In general, it appears that the current set of biological control agents will not cause further substantial reductions in yellow starthistle populations in California beyond the 50% already observed. This is reinforced by field data suggesting that the combined action of the four herbivores is inversely density-dependent in nature (Fig. 9, data from Pitcairn et al., 2002). Interestingly, anecdotal reports from the Pacific Northwest suggest that *E. villosus* has caused significant local reductions in yellow starthistle populations (E. Coombs, Oregon Department of Agriculture, and G. Piper, Washington State University, personal communication), possibly because the growing seasons in Oregon and Washington are shorter than in California, thereby limiting compensation by yellow starthistle. If so, seed destruction in such areas may prove to be an effective control strategy. This scenario was not investigated specifically, but GIS results shown in Fig. 8 suggest that *E. villosus* is more common and seed production and seed bank levels are not as high in the cooler, wetter areas of our study.

Recently, a new natural enemy, a leaf-rust fungus (*Puccinia jaceae* Oth var. *solstitialis* Savile), was approved and released in California against yellow starthistle (Woods et al., 2004). It is hoped that infection by this disease will complement the attack by the seed-feeding insects. In addition, a root-feeding weevil (*Ceratopion basicorne* (Illiger); Coleoptera: Apionidae) is under consideration for introduction. Both of these agents reduce photosynthetic rates either directly by reducing the effective leaf area or indirectly via damage to the root system. This injury would compromise the weed's ability to compete with the annual grasses and, later, to compensate for seed destruction by the capitulum-feeding insects. Their combined action may be similar to the action of the Klamath weed beetle (*Chrysolina quadrigemina* (Suffrain)) whose larvae defoliated its host plant causing reduced root development that increased whole plant stress leading to the successful control of

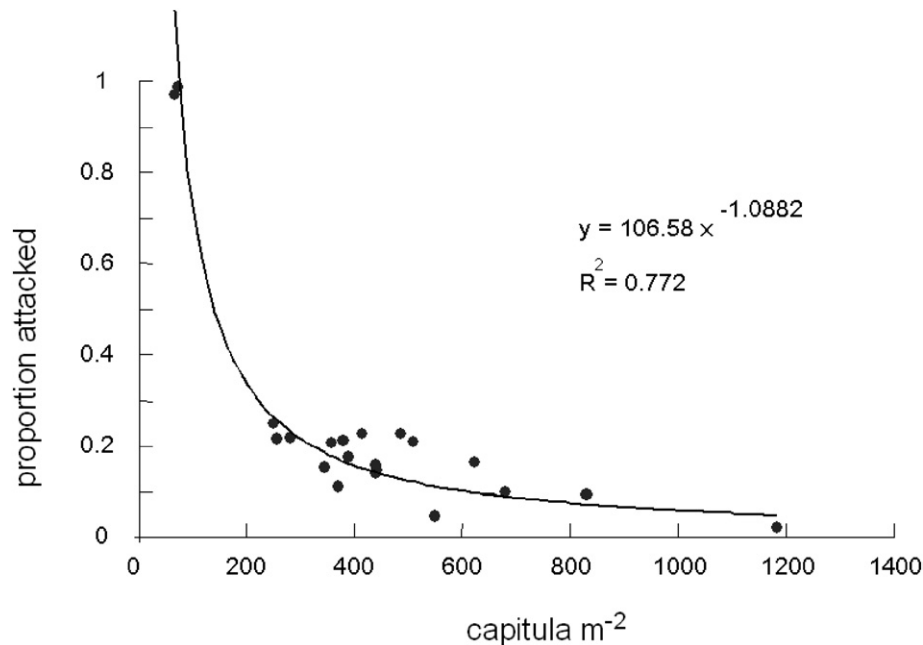


Fig. 9. The proportion of capitula attacked by all insects and capitulum density at three locations (Placer, Solano, and Yolo counties) in northern California during 1995–2001 (data from Pitcairn et al., 2002).

Klamath weed (St. Johnswort; *Hypericum perforatum* L.) in California (Huffaker and Kennett, 1959). Under Mediterranean climates with hot, dry summers, herbivores and diseases that severely weaken or kill plants after full investments in vegetative growth would appear to have the greatest impact on the plant's ability to compensate for seed destruction.

In yellow starthistle, the notion that the introduction of additional capitulum-feeding species for biological control would result in increased control was not borne out, as only a subset of species appear to cause significant seed destruction. To investigate these issues in further detail requires more refined estimates of the biological parameters for all of the herbivores than were available to us. Yet, despite the deficiencies in our knowledge regarding the biology of the introduced capitulum-feeding insects, the model appears to do a good job in explaining the relative contribution of each species to the reduction of yellow starthistle.

The use of GIS to provide a regional perspective of yellow starthistle abundance and the impact by the capitulum-feeding insects is new. It provides a system for prospectively guiding biological control efforts regionally by evaluating the impact of future natural enemies before their introduction. This information may help determine which species should be released, and to assess the sequence and timing of the releases (cf. McEvoy and Coombs, 1999). However, we caution that even the best models will never remove all of the uncertainty of biological control introductions, but they may reveal possible consequences and potential problems that otherwise might not be considered. To accom-

plish this synthesis, however, requires comprehensive age-specific life-table studies to quantify the biology and temperature relationships for each species. The work of Messenger (1964) provides an appropriate model for this work. Information obtained from this basic study can be quickly included to update weather-driven, physiologically based GIS models for local, metapopulation, and regional analyses (Gutierrez et al., 1999).

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